Atti Soc. it. Sci. nat. Museo civ. Stor. nat. Milano, 149 (II): 239-252, Giugno 2008

Simone Maganuco*, Andrea Cau** & Giovanni Pasini***

New information on the abelisaurid pedal elements from the Late Cretaceous of NW Madagascar (Mahajanga Basin)

Abstract - An abelisaurid ungual phalanx of pedal digit III from the Late Cretaceous of NW Madagascar is here figured and described for the first time. Other materials include pedal phalanges whose figures and description increase the knowledge on the pes variability of the Malagasy Abelisauridae (e.g., ungual I and phalanx III-1 proportions and structures), support the identification of the pedal elements (e.g., phalanx III-2) recently proposed by Carrano (2007), and render questionable the attribution of some isolated elements to the species *Majungasaurus crenatissimus*.

Key words: Madagascar, Late Cretaceous (Maastrichtian), Abelisauridae, pes, ungual phalanx of digit III, *Majungasaurus*.

Riassunto - Nuovi dati sulla conformazione del piede degli abelisauridi del Cretacico superiore del Madagascar nord-occidentale (Bacino di Mahajanga).

Viene qui descritta e figurata per la prima volta la falange ungueale del III dito del piede di un abelisauride del Cretacico superiore del Madagascar nord-occidentale. Gli altri elementi del piede presi in esame forniscono ulteriori dati sulla variabilità all'interno degli abelisauridi malgasci (ad esempio, in merito alle proporzioni e alle strutture dell'ungueale I e della falange III-1), nuove informazioni a supporto dell'identificazione degli elementi (ad esempio, la falange III-2) recentemente proposta da Carrano (2007) e rendono discutibile l'attribuzione di alcuni degli elementi isolati alla specie *Majungasaurus crenatissimus*.

Parole chiave: Madagascar, Cretacico superiore (Maastrichtiano), Abelisauridae, pes, falange ungueale del III dito, *Majungasaurus*.

Introduction

Recently, Sampson & Krause (2007) edited a landmark monograph representing a summary of the current knowledge pertaining to the abelisaurid theropod *Majun-*

* Museo di Storia Naturale di Milano, Corso Venezia 55, 20121 Milano, Italy; Dipartimento di Scienze della Terra, Università degli studi di Firenze, Italy; e-mail: simonemaganuco@iol.it (corresponding author)
** Museo di Storia Naturale di Milano, Corso Venezia 55, 20121 Milano, Italy,
e-mail: cauand@gmail.com
*** Museo Civico dei Fossili di Besano, Via Prestini 5, 21050 Besano (Varese), Italy,
e-mail: museocivicodibesano@tiscali.it

gasaurus crenatissimus, from the Late Cretaceous of Madagascar. The significant monograph initiated the basis for re-examining the material provisionally catalogued as belonging to this dinosaur species housed in the Vertebrate Paleontological Collection of the Museo di Storia Naturale di Milano, consisting of numerous isolated teeth (part of which published by Fanti & Therrien, 2007) and some pedal elements (only briefly mentioned in the unpublished M. Sc. thesis by Fanti, 2005). In the present article we focus our attention on those pedal elements. It is not the purpose of this article to re-describe the homologous elements already well-described by Carrano (2007). The aim of this paper is to contribute complete description of an abelisaurid ungual phalanx of digit III (not available in Carrano's description) and briefly deal with other collected pedal phalanges emphasizing the variability (with its possible taxonomic implications) or features of these specimens which will alleviate in the diagnosis of the hind limb material of abelisaurid taxa and also in identification of isolated material (e.g., Novas & Bandyopadhyay, 2001; Carrano *et al.*, 2002; Novas *et al.*, 2004; Novas *et al.*, 2005; Maganuco *et al.*, 2007).

Material and methods

The specimens are catalogued in the Vertebrate Palaeontological Collection of the Museo di Storia Naturale di Milano (acronym MSNM V).

In this article the systematic terminology of Wilson *et al.* (2003) and Carrano (2007) has been followed.

Institutional abbreviations: FMNH, Field Museum of Natural History, Chicago, IL; GSI, Geological Survey of India, Kolkata; UA, Université de Antananarivo, Antananarivo, Madagascar.

Geographical and geological provenance of studied specimens

The specimens were collected as surface finds during October 2001 joint expedition conducted by palaeontologists from the Museo di Storia Naturale di Milano (Italy) and the Museo Civico dei Fossili di Besano (Varese, Italy), in agreement with the Ministère de l'Énergie et des Mines and Direction des Mines et de la Géologie de Madagascar (Antananarivo).

All the specimens but MSNM V6418 come from the same Mahajanga Basin deposits S to the RN4 and Berivotra village (Mahajanga prov., NW Madagascar) formerly prospected by: Lavocat in 1954 (Lavocat 1955a, b, c; and 1957), Muséum National d'Histoire Naturelle of Paris in 1974 (Russell *et al.*, 1976), National Science Museum of Tokyo in 1973-75 (Obata & Kanie, 1977; Asama, 1977; and Asama *et al.*, 1981); Stony Brook University and University of Antananarivo joint expeditions, formally Mahajanga Basin Project since 1993 to present, (see Krause *et al.*, 2007: fig. 2). From 2000 onwards the MSNM and Museo Civico dei Fossili di Besano (Varese, Italy) started joint expedition in agreement with the Service des Mines de Madagascar (Antananarivo) - focussing particularly on the invertebrate fauna from marine facies of Berivotra Formation (Garassino & Pasini, 2003). The covered area of the collecting corresponds to an area less than 1 kmq. The combined information about distance among the specimens (found sparse), specimen size, and specimen identification (e.g., five asymmetrical unguals and two phalanges III-1 are represented in a sample consisting of nine specimens only) supports the presence of

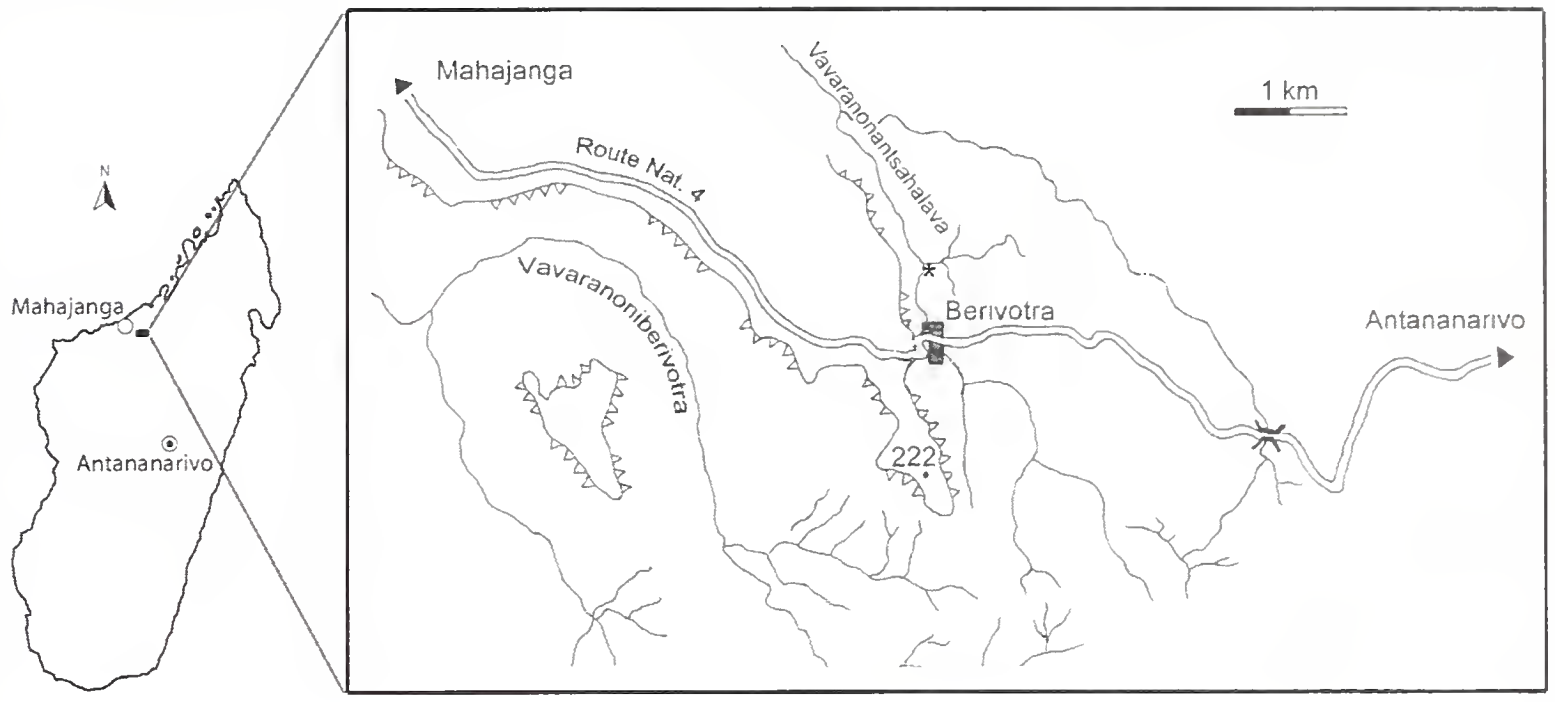

Fig. 1 - Geographic map of the fossil location near the village Berivotra; the main localities and landscape elements cited in the text are shown in the map. The asterisk marks the site from where the specimen MSNM V6418 was collected (modified from Garassino & Pasini, 2003: fig. 2; which is again based on the original drawing by Lavocat, 1955a).
Fig. 1 - Cartina geografica dei dintorni del villaggio di Berivotra, in cui sono evidenziati le principali località e i toponimi citati nel testo. L'asterisco indica la località da cui proviene l'esemplare MSNM V6418 (rielaborata e semplificata a partire da Garassino & Pasini, 2003: fig. 2, a sua volta basata sul disegno originale di Lavocat, 1955a).

at least three individuals. This renders impossible to establish if the specimens of similar size and compatible with a single pes belong to a single individual or not.

The specimen MSNM V6418 comes from the left bank of a small stream called "Vavaranonantsahalava" (local name already reported by Lavocat, 1955a: fig. 2), about 500 m NE to the Berivotra village (Fig. 1).

Following Rogers *et al.* (2007), the uppermost white sandstone unit (Anembalemba Member) of the Maevarano Formation from where these specimens were collected has been dated as Maastrichtian (ICS stage), 70.6-65.5 Ma (Gradstein *et al.*, 2004).

Systematic Palaeontology

Dinosauria Owen, 1842
Saurischia Seeley, 1888
Theropoda Marsh, 1881
Ceratosauria Marsh, 1884
Abelisauroidea Bonaparte, 1991
Abelisauridae Bonaparte and Novas, 1985
Gen. et sp. indet.

Comments - *Majungasaurus crenatissimus* is the only abelisaurid species from the Maevarano Formation (Late Cretaceous of Madagascar) reported up to today, but the diagnosis of the species does not include any pedal characters. None of our pedal elements corresponds to the pedal elements associated to diagnosable skeletal remains of the species (Carrano, 2007: 165). Therefore, we prefer to refer our isolated abelisaurid pedal elements to the Abelisauridae, pending articulated, complete, pedal material of this species. Similarly, in our opinion, the attribution of

the isolated pedal elements described by Carrano (2007) to *Majungasaurus crenatissimus* should be regarded with caution.

Described material - The following description of abelisaurid pedal elements is based on ten specimens: MSNM V5255, MSNM V5256, MSNM V5267, MSNM V5276, MSNM V5509, MSNM V5510, MSNM V6418, MSNM V6419, MSNM V6420, MSNM V6421 (Tab. 1).

Locality and Horizon - Near the village of Berivotra, Mahajanga Basin, NW Madagascar; Anembalemba Member of the Maevarano Formation, Late Cretaceous (Maastrichtian).

Description and comparisons

Non-ungual phalanges - All the collected non-ungual pedal phalanges belong to the digit III. As a matter of fact, they show all the features found by Novas *et al.* (2004) and Carrano (2007) in pedal phalanges of digit III of Indian and Malagasy abelisaurids supporting their identification as belonging to digit III: phalanges almost symmetrical; dorsoventrally depressed; with a crescent-shaped proximal articular surface that is dorsoventrally lower than wide and lacks a vertical ridge entirely; with proximal ends flared for articulation with the preceding metatarsal III or phalanx; and, in lateral view, dorsal margin more or less straight and ginglymus lacking a dorsally expanded articular facet, being even slightly more depressed than the rest of the dorsal margin of the bone (a condition contrasting with tetanuran theropods such as *Sinraptor*, *Allosaurus*, and *Tyrannosaurus*).

Pedal phalanges III-1 (specimens MSNM V5255 and MSNM V5510) - The specimen MSNM V5255 (Fig. 2 A-F) is a phalanx III-1 of the left pes, lacking most of the proximal articular surface. It has a D-shaped extensor pit. It well matches the morphology of the right phalanges III-1 UA Bv-1265 and FMNH PR 2429 referred to *Majungasaurus crenatissimus* (Carrano, 2007), being only more slender. A comparable slenderness can be seen in the abelisauroid specimens from the Maastrichtian Lameta Formation of India GSI K27/646 and GSI K27/525 figured by Novas *et al.*, (2004: fig. 30) and identified - the former tentatively - as III-1. We interpreted the specimen MSNM V5510 (Fig. 2 G-L) as another phalanx III-1. It is considerably larger than MSNM V5255 but equally slender, and has an extensor pit that is semi-elliptical rather than D-shaped as in MSNM V5255.

Pedal phalanx III-2 (specimen MSNM V5256) - In the specimen MSNM V5256 (Fig. 3 G-L), the left proximo-dorsal corner and the left condyle (lateral - see below) are missing, and the distal surface is partly eroded. The specimen MSNM V5256 closely resembles the specimen UA 9042, tentatively identified with caution by Carrano (2007: fig. 11) as the III-2, as well as the abelisauroid specimen GSI K27/653 identified by Novas *et al.* (2004: fig. 30 D) as III-2, being only a little bit stouter than both. Therefore, it can be identified as a phalanx III-2 of the left pes. The specimen MSNM V5256 differs from both UA 9042 and GSI K27/653 in lacking the extensor pit. This pit, however, although present in the phalanx III-2 referred to *Majungasaurus crenatissimus*, seems shallower in this phalanx than in other phalanges (Carrano, 2007: fig. 11). The distal heels in phalanx III-2 MSNM V5256 are abruptly demarcated from the shaft at their proximal edges. Carrano (2007) described a similar pattern of distal heels in the phalanx III-1 referred to *Majungasaurus crenatissimus*.

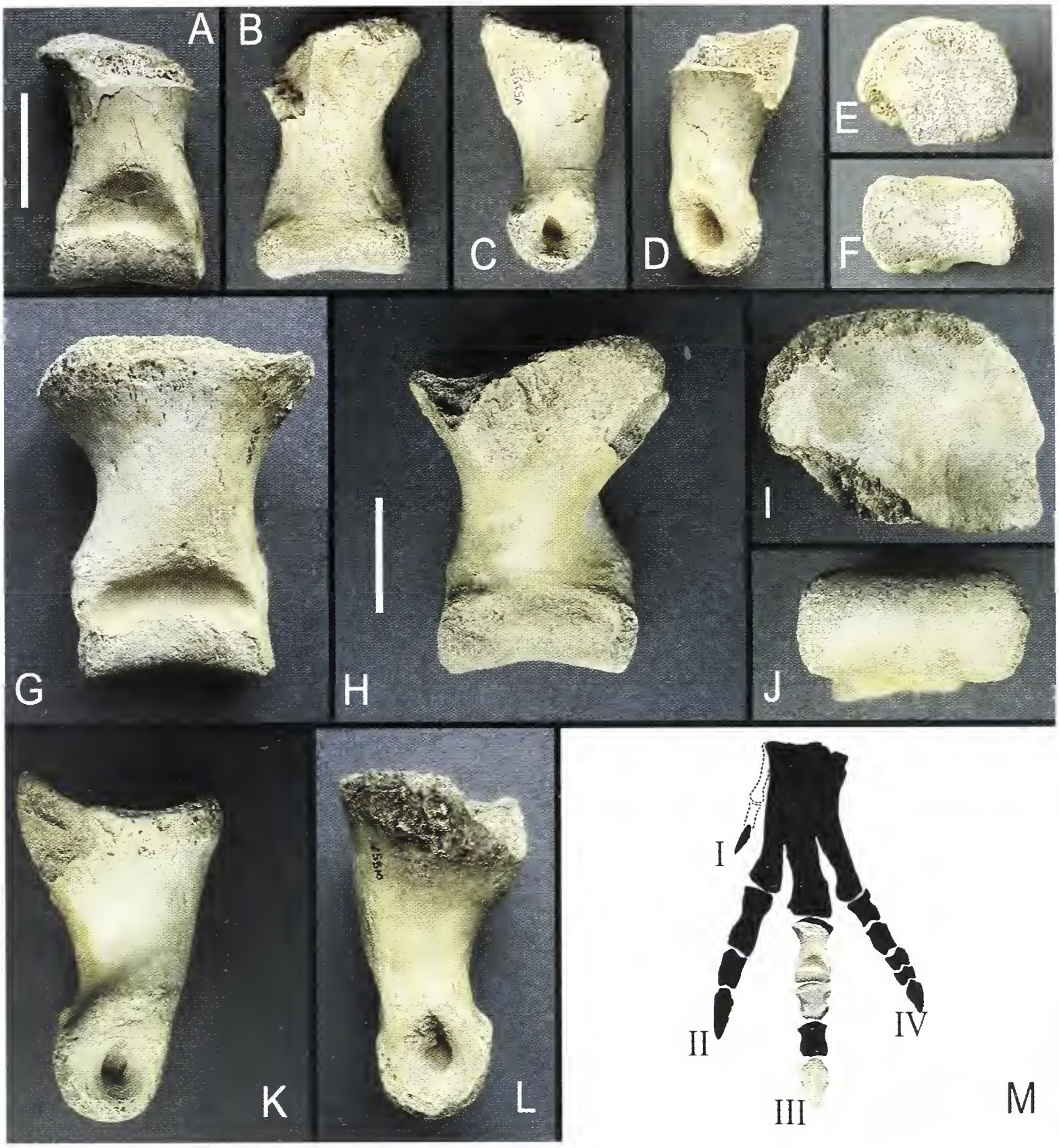

Fig. 2 - Abelisaurid pedal phalanges III-1 (A-L) and reconstructed abelisaurid digit III of the left pes in craniodorsal view (M). MSNM V5255: A) dorsal view; B) ventral view; C-D) lateral views; E) proximal view; F) distal view. MSNM V5510: G) dorsal view; H) ventral view; I) proximal view; J) distal view; K-L) lateral views. Scale bars equal 30 mm. In M) the pedal elements in silhouette are from Carrano (2007: fig. 11), and the phalanges of the digit III are based on specimens MSNM V5255 (III-1), MSNM V5256 (III-2), and MSNM V6418 (III-4), scaled up to correspond with the size of the elements represented in Carrano's reconstruction.

Fig. 2 - Falangi del piede di abelisauride (A-L) e ricostruzione del terzo dito del piede sinistro di abelisauride in norma craniodorsale (M). MSNM V5255: A) norma dorsale; B) norma ventrale; C-D) norme laterali; E) norma prossimale; F) norma distale. MSNM V5510: G) norma dorsale; H) norma ventrale; I) norma prossimale; J) norma distale; K-L) norme laterali. Le scale metriche equivalgono a 30 mm. In M) gli elementi in silhouette sono sono presi da Carrano (2007: fig 11), mentre le falangi del III dito corrispondono agli esemplari MSNM V5255 (III-1), MSNM V5256 (III-2) e MSNM V6418 (III-4), ridotte proporzionalmente, in modo da adattarle alle dimensioni degli elementi rappresentati nella ricostruzione di Carrano.

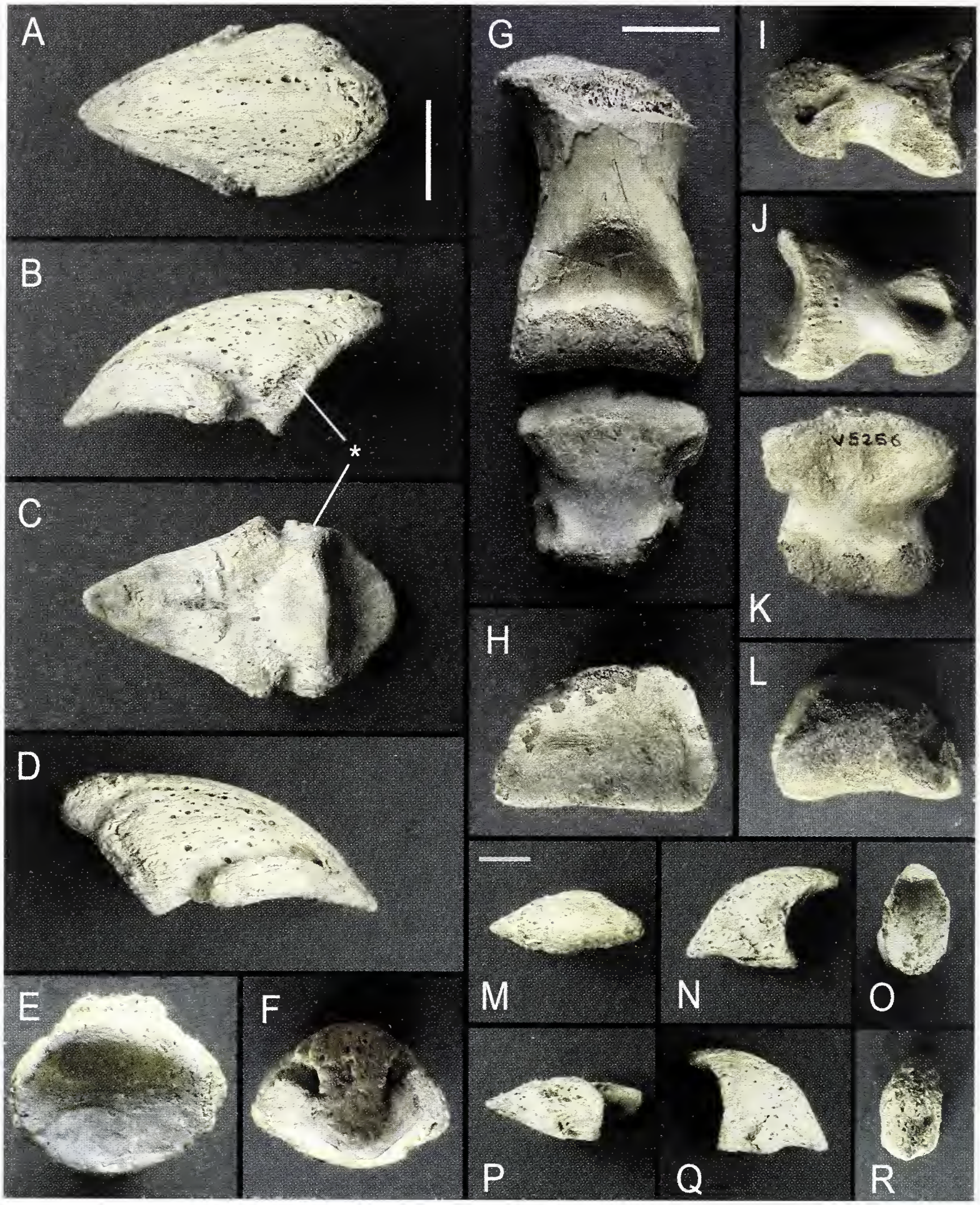

Fig. 3 - Abelisaurid pedal phalanges. Phalanx III-4 (MSNM V6418): A) dorsal view; B-D) lateral views; C) ventral view; E) proximal view; F) distal view. Left phalanx III-2 (MSNM V5256): G) dorsal view, with phalanx III-1 (MSNM V5255); H) proximal view; I-J) lateral views; K) ventral view; L) distal view. ?Left phalanx I-2 (MSNM V6419): M) dorsal view; N) ?medial view; O) proximal view; P) ventral view; Q) ?lateral view; R) distal view. The asterisk in B and C indicates a sub-triangular surface (see description). Scale bars equal 20 mm in A and 10 mm in M.

Fig. 3 - Falangi del piede di abelisauride. Falange III-4 (MSNM V6418): A) norma dorsale; B-D) norme laterali; C) norma ventrale; E) norma prossimale; F) norma distale. Falange III-2 del piede sinistro (MSNM V5256): G) norma dorsale, associata alla falange III-1 (MSNM V5255); H) norma prossimale; I-J) norme laterali; K) norma ventrale; L) norma distale. Falange I-2 del piede ?sinistro (MSNM V6419): M) norma dorsale; N) norma ?mediale; O) norma ventrale; P) norma ?laterale; Q) norma distale; R) norma prossimale. L'asterisco in B e C indica una superficie sub-triangolare (si veda la descrizione). Le scale metriche equivalgono a 20 mm in A e a 10 mm in M.

Although it is impossible to establish if the specimens MSNM V5255 and MSNM V5256 belong to a single individual (see geographical and geological provenance of studied specimens), they perfectly articulate each other, and seem to belong to individuals having approximately the same body size (Fig. 3 G). Together with the specimen MSNM V6418, they form a partial, composite digit III (Fig. 2 M) with slightly different proportions (i.e., longer and slender) from the reconstructed digit III in Carrano (2007), emphasizing the variability within the abelisaurid pedal material from the Maevarano Formation.

Ungual phalanges - Some of the collected abelisaurid pedal phalanges possibly represent all the four unguals from digits I-IV.

Ungual phalanx of digit I (MSNM V6419) - The specimen MSNM V6419 (Fig. 3 M-R) is a very small, deep, short, and nearly symmetrical ungual that well matches the morphology of pedal phalanx I-2 of *Majungasaurus crenatissimus* (Carrano, 2007). MSNM V6419 differs from the latter in having a flexor tubercle on the proximoventral surface (see below). The shortness of the specimen MSNM V6419 (the length of the ventral surface is only slightly greater than the height of the proximal surface) may eventually distinguish it from the specimen UA Bv-532 (Carrano, 2007: fig. 11): unfortunately, we had not the opportunity to see additional photos of that specimen but the small image in dorsal view available in the publication. Similarly shortened pedal unguals can be seen in the digit IV of the abelisaurid *Aucasaurus* (Coria *et al.*, 2002: fig. 4), but not in digits I and II. On the contrary, in other abelisauroid (Novas & Bandyopadhyay, 2001; Novas *et al.*, 2004: fig. 31 A) and tetanuran (e.g., Currie & Zhao, 1993: fig. 28 D; Brochu, 2003; Kobayashi & Barsbold, 2005) theropods, the length of the ventral margin of the pedal unguals (I included) is clearly greater than the height of the proximal surface. The same condition occurs even in taxa showing very shortened both manual and pedal unguals, such as the basal coelurosaur *Juravenator* (Göhlich & Chiappe, 2006).

As mentioned above, the specimen MSNM V6419 bears a faintly developed, flattened flexor tubercle on the proximoventral surface, whereas in the specimens referred to *Majungasaurus crenatissimus* UA Bv-532 and UA Bv-1658 "ventrally there is no flexor tubercle, but rather a shallow, flattened fossa" (Carrano, 2007: 174). Carrano (2007: 176) also indicated the absence of flexor tubercles as a general feature of pedal unguals of *Majungasaurus*. This is the case in most abelisauroid pedal unguals (Novas & Bandyopadhyay, 2001; Carrano *et al.*, 2002; Novas *et al.*, 2004; Novas *et al.*, 2005). However, a certain degree of variability regarding this feature can be noted: a slight eminence corresponding to a low proximoventral flexor tubercle was also reported in an abelisauroid pedal ungual from the Cenomanian of Morocco (Novas *et al.*, 2005) and in a basal abelisauroid from the Bathonian of Madagascar (Maganuco *et al.*, 2007); and a small tubercle, mainly like a thickening of the ventral side of pedal ungual I is present in *Aucasaurus* (Coria, pers. comm., 2008). Besides the lateral furrows bifurcating at mid-length towards the proximal articular surface visible in MSNM V6419 are common in abelisauroid pedal unguals (Novas & Bandyopadhyay, 2001; Maganuco *et al.*, 2007: 266). According to Coria *et al.* (2002), it is still not clear whether the digits of the hand of *Aucasaurus*, the best known abelisaurid manus, bear claws or not; both the known manual and pedal ungual of *Masiakasaurus knopfleri* are different in shape and the

maximum adult body size attained by that species (Carrano *et al.*, 2002) does not match with the size of a similarly shaped ungual phalanx. Therefore, on the basis of the present knowledge, we provisionally consider our specimen as a pedal ungual of the digit I of an abelisaurid theropod.

Ungual of digit III (specimen MSNM V6418) - The specimen MSNM V6418 (Fig. 3 A-F) is a symmetrical ungual, that we refer to the digit III. It is almost complete, except the distalmost three mm of the tip and part of the ventral half of the proximal articular surface, partially reinforced in plaster to avoid their detachment. As stated above, the pedal phalanx III-4 was not present in the sample described by Carrano (2007). The general morphology (i.e., shape, proportions, pattern of furrows) strongly recalls that of the Indian specimen GSI K27/634 (Novas & Bandyopadhyay, 2001: fig. 2 A-D), the only other abelisaurid III-4 pedal phalanx described up to date. The triangular proximal surface slopes proximodorsally forming an angle of about 35° respect to the ventral surface of the bone. It is slightly concave, and very faintly divided in two sub-equal articular surfaces. The articular facet is a little bit broader than tall. Numerous foramina are present, especially on the dorsal and lateral surfaces. Dorsally the extensor tubercle is rugose and projects proximally overhanging the proximal articular facet. A pair of deep furrows on lateral sides bifurcates at mid length. The dorsal furrows are more vascularized but shallower than the ventral ones. The proximalmost extent of the ventral furrows is separated from the lateral margins of the proximal articular surface by a pair of flat, rugose, sub-triangular surfaces (Fig. 3 B, C). Those sub-triangular surfaces seem to be absent in the ungual III GSI K27/634 from the Lameta Formation (Novas & Bandyopadhyay, 2001: fig. 2 A-D), which seems to have also ventral furrows proximally shallower than in MSNM V6418. Proximally, the ventral furrows of MSNM V6418 move towards each other on the ventral surface, meeting in the middle in a single proximodistally elongate furrow, which deepens distally and ends at the level of the distal third of the ungual. A flexor tubercle is absent on the ventral surface.

Unguals of digits II and / or IV - The specimens MSNM V5267, V5276, V5509, V6420 (Fig. 4 G-L), and V6421 (Fig. 4 A-F) are highly asymmetrical unguals (i.e., those pertaining to the II and IV digits), lacking flexor tubercle and having a triangular arrangement of vascular grooves and a ventral surface excavated with a narrow and deep furrow (Novas & Bandyopadhyay, 2001). In general morphology, they match well with the morphology of the asymmetrical unguals referred to *Majungasaurus crenatissimus* as described by Carrano (2007), and resemble in shape with both FMNH PR 2434 (Carrano, 2007: fig. 13) and abelisaurid asymmetrical unguals from India and Patagonia (Novas & Bandyopadhyay, 2001). These unguals are more robust than the slender abelisaurid pedal ungual from Africa (Novas *et al.*, 2005). In our collection of asymmetrical unguals, two different set of unguals can be separated out on the basis of morphology: the specimens MSNM V5267 and V6421 (Fig. 4 F) are more asymmetrical, with a dorsoventral axis of the proximal surface tilted towards the surface with the rounded bump, and have a broader proximal articular surface, with proximal articular facets corresponding to the condyles of the preceding phalanx sub-equal in depth and separated by a wide, very low ridge; the specimens MSNM V5276, V5509, and V6420 (Fig. 4 L) are comparatively symmetrical, with a proximal articular surface taller and sepa-

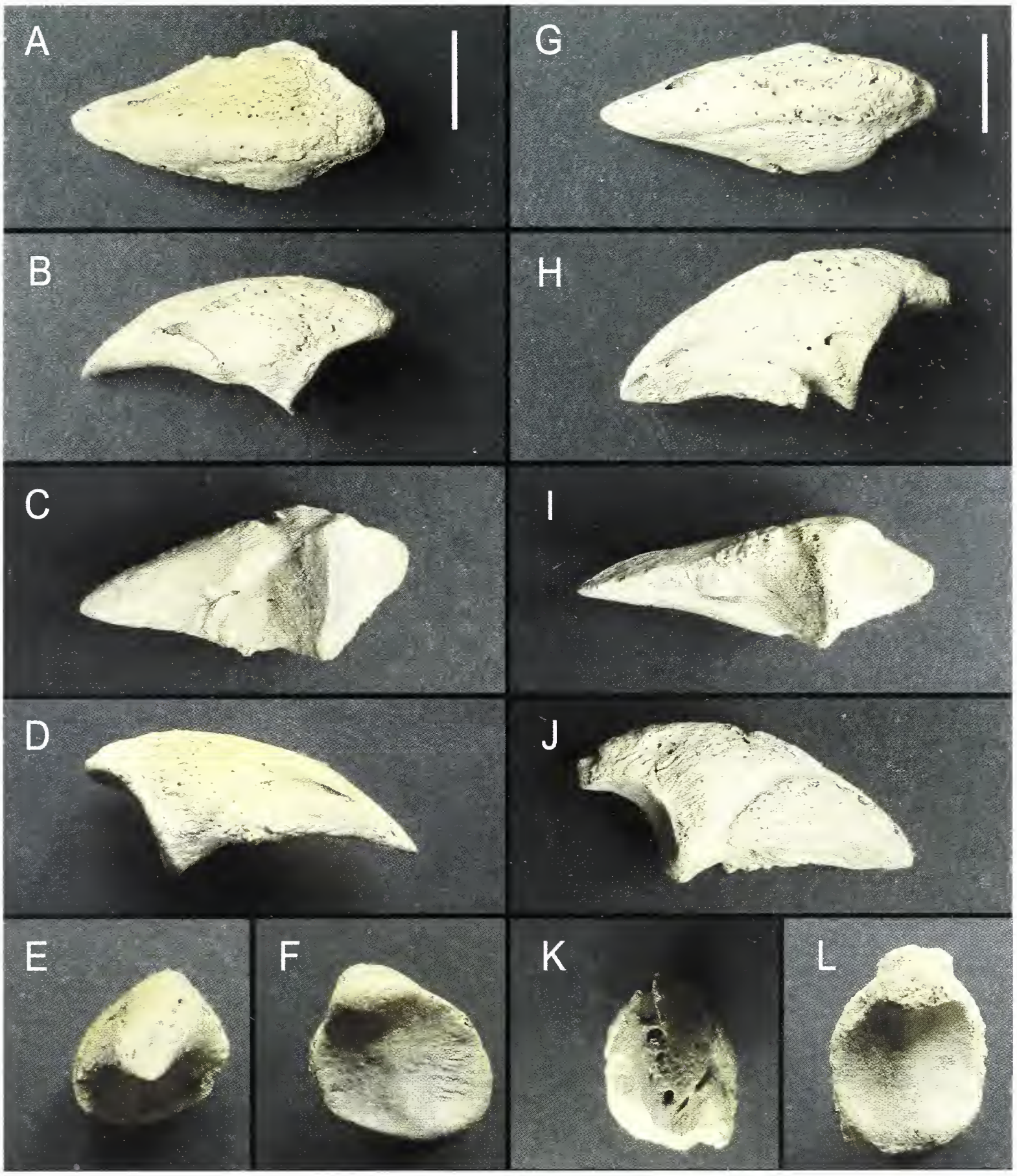

Fig. 4 - Asymmetrical abelisaurid pedal ungual phalanges (see the text for explanation on the tentative identification here proposed). ?Left phalanx ?II-3 (MSNM V6421): A) dorsal view; B) ?medial view; C) ventral view; D) ?lateral view; E) distal view; F) proximal view. ?Left phalanx ?IV-5 (MSNM V6420): G) dorsal view; H) ?lateral view; I) ventral view; J) ?medial view; K) distal view; L) proximal view. Scale bars equal 20 mm.

Fig. 4 - Falangi ungueali asimmetriche del piede di abelisauride (per spiegazioni sull'ipotetica identificazione qui proposta si veda il testo). Falange ?II-3 del piede ?sinistro (MSNM V6421): A) norma dorsale; B) norma ?mediale; C) norma ventrale; D) norma ?laterale; E) norma distale; F) norma prossimale. Falange ?IV-5 del piede ?sinistro (MSNM V6420): G) norma dorsale; H) norma ?laterale; I) norma ventrale; J) norma ?mediale; K) norma distale; L) norma prossimale. Le scale metriche equivalgono a 20 mm.

rated by a weak ridge with an almost vertical dorsoventral axis, and with proximal articular facets corresponding to the condyles of the preceding phalanx sub-equal in width but not in depth, the one towards the surface with the rounded bump being deeper than the other.

Following Carrano *et al.* (2002) and Novas *et al.* (2004), in which metatarsal IV and non-ungual phalanges of digit IV of abelisauroid theropods are described as distinctly transversely narrow and dorsoventrally deep, with a medial condyle more elongate than the lateral one (in sharp contrast with those of tetanuran theropods such as *Sinraptor*, *Allosaurus*, *Tyrannosaurus*, and *Deinonychus*, in which the phalanges of the digit IV are proportionally lower and wider); and following the description and tentative reconstruction of the pes by Carrano (2007), in which a tilted long axis is described for the ungual phalanx of the digit II and in digit IV the lateral condyle is reported to be more markedly shallower and smaller than the medial; so the specimens MSNM V5267 and V6421 may be tentatively considered as unguals II, whereas the specimens MSNM V5276, V5509, and V6420 as unguals IV. This contrasts with the identification proposed by Novas & Bandyopadhyay (2001), who identified the very deep and transversely narrow abelisaurid pedal ungual GSI K27/633 as belonging to digit II on the basis of its resemblance with the ungual of the digit II of the tetanuran *Sinraptor* (Currie & Zhao, 1993). Interestingly, the unguals II and IV are virtually symmetrical on the right pes of the abelisaurid *Aucasaurus garridoi*, whereas on the left pes they both are equally asymmetrical (Coria, pers. comm., 2008). Therefore, in the absence of described articulated, complete, pedal material of Malagasy abelisaurids, in our opinion it is impossible to ascertain if the morphological variation shown by our asymmetrical unguals is due to intra- or interspecific variability or to a real different position in the pes (i.e., to their belonging to the II or IV digit).

Tab. 1 - Basic measurements of the phalanges described in the text. Measurements are in mm. One asterisk (*) indicates estimated measurements. Two asterisks (**) indicate that the measurement refers to the preserved portion of the incomplete bone.
Tab. 1 - Misure principali delle falangi descritte nel testo. Le misure sono in mm. Un asterisco (*) indica che la misura corrisponde a una stima. Due asterischi (**) indicano invece che la misura si riferisce alla porzione conservata dell'osso incompleto.

Specimen	Maximum length	Maximum width	Maximum height
MSNM V5255	60	40**	31
MSNM V5256	36	35	21
MSNM V5267	42	21	24
MSNM V5276	52	18	24
MSNM V5509	51	18	23
MSNM V5510	74	57	42
MSNM V6418	57*	32	25
MSNM V6419	29	11	19
MSNM V6420	61	23	28
MSNM V6421	56	26	24

Conclusions

The specimens described here provided an important addition to the description of the appendicular skeleton of the abelisaurid theropods from the Maevarano Formation (Late Cretaceous of Madagascar) published by Carrano (2007). The formerly unknown ungual phalanx of the digit III of the pes is fully described, and appears to be strongly similar to that of the Indian abelisaurids (Novas & Bandyopadhyay, 2001). Some additional information increasing the knowledge on the pes variability within the Malagasy abelisaurids are provided (e.g., presence/absence of flexor tubercle on ungual I and extensor pit on phalanx III-2; shape of the extensor pit in phalanges III-1; ungual I and phalanx III-1 proportions), further substantiating Carrano's (2007) interpretations (e.g., identification of phalanx III-2) and pes reconstruction but also rendering questionable the taxonomic attribution of the material at specific level.

As briefly mentioned in the comments above, Carrano (2007) reported that only pedal elements II-1, IV-2, and IV-3 were associated to a partial skeleton of *Majungasaurus crenatissimus* (specimen FMNH PR 2278); pedal elements II-1, II-2, III-1(or III-2?), IV-1, and IV-2 come from a single quarry horizon along with a nearly complete skull belonging to this species; the remaining pedal elements, however, were found isolated. No apomorphies other than abelisaurid synapomorphies are recognized among these isolated specimens. Indeed, the revised diagnosis of the species (Krause *et al.*, 2007) does not include any pedal feature. Therefore, the isolated specimens should be diagnosed as Abelisauridae gen. et sp. indet., or at most referred with caution to cf. *M. crenatissimus*, being the only abelisaurid species from the Anembalemba Member of the Maevarano Formation reported up to today.

Similarly, none of our pedal elements is homologous to the pedal elements associated to diagnosable skeletal remains of the species in Carrano (2007), so that our material could be as well referred to *Majungasaurus* only on the basis of its occurrence in the same strata.

The morphological variability found in pedal unguals of digit I and pedal phalanges III-1 indicates a higher diversity among the abelisaurid material from the Maevarano Formation than previously recognized. As stated by Carrano (2007), the proportional differences among the phalanges may have been reconducted to some dimorphism in *Majungasaurus crenatissimus*. However, it cannot be ruled out that this variability is above the species level (e.g., the pedal ungual I MSNM V6419 could be diagnosed by the presence of a flexor tubercle and the lowest h/l ratio among described or figured theropods). In this case, it would be impossible to establish, for example, which of the isolated pedal unguals of digit I belongs to *Majungasaurus crenatissimus*, and which one to a second species of abelisaurid theropod.

For all these reasons, on the basis of the present evidence we prefer to regard all the isolated abelisaurid pedal elements from the Maevarano Formation as belonging to Abelisauridae gen. et sp. indet.

Regarding the isolated asymmetrical unguals, their incorporation to the digit II or IV has been investigated; only tentative suggestion can be formulated at present (although consistent with the morphology of abelisauroid non-ungual pedal phalanges and metatarsals), pending recovery of articulated, complete, pedal material.

Acknowledgements

We are grateful to the Ministère de l'Energie et des Mines and Direction des Mines et de la Géologie de Madagascar (Antananarivo), for the collaboration. The manuscript greatly benefited from reviews by Fernando E. Novas (Museo Argentino de Ciencias Naturales) and Saswati Bandyopadhyay (Geological Studies Unit, Indian Statistical Institute). We are indebted to Rodolfo Coria (Museo Municipal "Carmen Funes") for the unpublished information on the pes of *Aucasaurus*. Photos are by SM.

References

Asama Y., 1977 – The 1973 and 1975 paleontological expeditions of Madagascar by the National Science Museum, Tokyo. *National Science Museum Bulletin Series C (Geology)*, 3: 103-106.

Asama Y., Obata I. & Kanie Y., 1981 – Paleontological investigations of Madagascar by the National Science Museum Team, Tokyo. *Recent Programs National Science Japan*, 6: 163-174.

Brochu C. A., 2003 – Osteology of *Tyrannosaurus rex*: insights from a nearly complete skeleton and high-resolution computed tomographic analysis of the skull. *Journal of Vertebrate Paleontology*, 22 (4) (Supplement): 1-138.

Carrano M. T., 2007 – The appendicular skeleton of *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. In: *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. Sampson S. D. & Krause D. W., (eds.). *Society of Vertebrate Paleontology, Memoir 8*: 164-179.

Carrano M. T., Sampson S. D. & Forster C. A., 2002 – The osteology of *Masiakasaurus knopfleri*, a small abelisauroid (Dinosauria: Theropoda) from the Late Cretaceous of Madagascar. *Journal of Vertebrate Paleontology*, 22: 510-534.

Coria R. A., Chiappe L. M. & Dingus L., 2002 – A new close relative of *Carnotaurus sastrei* Bonaparte 1985 (Theropoda: Abelisauridae) from the Late Cretaceous of Patagonia. *Journal of Vertebrate Paleontology*, 22: 460-465.

Currie P. J. & Zhao X. J., 1993 – A new carnosaur (Dinosauria, Theropoda) from the Jurassic of Xinjang, People's Republic of China. *Canadian Journal of Earth Sciences*, 30: 2037-2081.

Fanti F., 2005 – Stratigraphy and Paleontology of the Cretaceous Layers of Berivotra (Mahajanga, Madagascar): Paleobiogeographic Implications. *Unpublished M. Sc. thesis, University of Bologna*: 1-375.

Fanti F. & Therrien F., 2007 – Theropod tooth assemblages from the Late Cretaceous Maevarano Formation and the possible presence of dromaeosaurids in Madagascar. *Acta Palaeontologica Polonica*, 52 (1): 155-166.

Garassino A. & Pasini G., 2003 – First record of Calappoidea, Portunoidea and Dromioidea in the Upper Cretaceous (Upper Maastrichtian) of NW Madagascar. *Bulletin of the Mizunami Fossil Museum*, 30: 121-135.

Göhlich U. B. & Chiappe L. M., 2006 – A new carnivorous dinosaur from the Late Jurassic Solnhofen archipelago. *Nature*, 440: 329-332.

Gradstein F. M., Ogg J. G. & Smith A. G., (eds.), 2004 – A Geologic Time Scale 2004. *Cambridge University Press*.

Kobayashi Y. & Barsbold R., 2005 – Re-examination of a primitive ornithomimosaur, *Garudimimus brevipes* Barsbold, 1981 (Dinosauria: Theropoda), from the Late Cretaceous of Mongolia. *Canadian Journal of Earth Sciences*, 42: 1501-1521.

Krause D. W., Sampson S. D., Carrano M. T. & O'Connor P. M., 2007 – Overview of the history of discovery, taxonomy, phylogeny, and biogeography of *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. In: *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. Sampson S. D. & Krause D. W., (eds.). *Society of Vertebrate Paleontology, Memoir 8*: 1-20.

Lavocat R., 1955a – Etudes des gisements de Dinosauriens de la région de Majunga (Madagascar). *Travaux du Bureau Géologique*, 69. 1-19.

Lavocat R., 1955b – Sur une portion de mandibule de Théropode provenant du Cétacé supérieur de Madagascar. *Bulletin du Muséum National d'Histoire Naturelle,* 27: 256-259.

Lavocat R., 1955c – Les recherches de reptiles fossiles à Madagascar. *Le Naturaliste Malgache* VII (2): 203-207.

Lavocat R., 1957 – Sur les couches à dinosauriens de Madagascar. CCTA and Service Géologique de Madagascar. *Comptes Rendus. Comité régionaux Centre Est et Sud Conférence de Tananarive, Avril 1957, Geology, Second Volume*: 363-364.

Maganuco S., Cau A., Pasini G. & Dal Sasso C., 2007 – Evidence of large theropods from the Middle Jurassic of the Mahajanga Basin, NW Madagascar, with implications for ceratosaurian pedal ungual evolution. *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale in Milano*, 148 (II): 261-271.

Novas F. E. & Bandyopadhyay S., 2001 – Abelisaurid pedal unguals from the Late Cretaceous of India. *VII International Symposium on Mesozoic Terrestrial Ecosystems, Buenos Aires, 30-6-2001*: 145-149.

Novas F. E., Agnolin F. L. & Bandyopadhyay S., 2004 – Cretaceous theropods from India: A review of specimens described by Huene and Matley (1933). *Revista Museo Argentino de Ciencias Naturales*, n.s., 6 (1): 67-103.

Novas F. E., Dalla Vecchia F. & Pais D. F., 2005 – Theropod pedal unguals from the Late Cretaceous (Cenomanian) of Morocco, Africa. *Revista Museo Argentino de Ciencias Naturales*, n.s., 7 (2): 167-175.

Obata I. & Kanie Y., 1977 – Upper Cretaceous dinosaur-bearing sediments in Majunga region, northwestern Madagascar. *National Science Museum Bulletin Series C (Geology)*, 3: 161-172.

Owen R., 1842 – Report on British fossil reptiles. Part II. *Reports of the British Association for the Advancement of Science*, 11: 60-204.

Rogers R. R., Krause D. W., Curry Rogers K., Rasoamiaramanana A. H. & Rahantarisoa L., 2007 – Paleoenvironment and paleoecology of *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. In: *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. Sampson S. D. & Krause D. W., (eds.). *Society of Vertebrate Paleontology, Memoir 8*: 21-31.

Russel D., Taquet P. & Thomas H., 1976 – Nouvelles récoltes de Vetebrés dans les terrains continentaux du Crétacé supérieur de la région de Majunga (Madagascar). *Comptes Rendus Sommaire des Séances et Bulletin de la Societé Géologique de France*, 5: 205-208.

Sampson S. D. & Krause D. W., 2007 – *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. *Society of Vertebrate Paleontology, Memoir 8*: 1-184.

Seeley H. G., 1888 – The classification of the Dinosauria. *Reports from the British Association for the Advancement of Science, 57th Meeting, Manchester*, 1887: 698-699.

Ricevuto: 28 gennaio 2008
Accettato: 15 maggio 2008